

THE RELATIONSHIP OF THE MESOZOIC BIVALVE *ATRETA* TO THE DIMYIDAE

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ABSTRACT. Material recently collected from the Lower Lias (Lower Jurassic) of South Wales shows evidence of dimyarian musculature in *Atreta intusstriata* (Emmrich) proving that the previous assignment of *Atreta* to the monomyarian Plicatulidae Watson, 1930, by Cox (1964) is incorrect. The genus is therefore reassigned to the Dimyidae Fischer, 1886. A lectotype and paralectotypes are designated from material located in the Emmrich collection at the Geiseltal Museum, Halle, Germany.

ETALLON (1862) erected *Atreta* and described the main diagnostic features, namely two projecting teeth, dimyarian musculature and anastomosing riblets in the right valve. Five species were listed as belonging to this genus: *Ostrea blandina* d'Orbigny, 1849, *Spondylus dichotomus* Buvignier, 1852, *Plicatula striatissima* Quenstedt, 1858, *Crania humbertina* Buvignier, 1852, and *Atreta imbricata* sp. nov. The last two were described, but none was figured and no type species selected. Rollier (1917) later invalidly selected *Atreta jurensis* Etallon, 1862, as type species.

The designation of *Ostrea blandina* as type species was made by Cox (1964), who considered Etallon's generic diagnosis extremely doubtful due to the generally poor preservation of the material available. He noted also that several authors after Etallon had failed to observe any musculature in species of this genus. Although he admitted that the main characteristics were allied to the Dimyidae, he nevertheless placed *Atreta* in the Plicatulidae due to his doubts about the presence of dimyarian musculature.

RELATIONSHIP OF THE DIMYIDAE TO OTHER BIVALVE FAMILIES

The Dimyidae comprises species which are suborbicular in outline, cemented by the right valve and with dimyarian musculature. Thiele (1935), Newell *in* Moore (1969) and Vokes (1980) placed the Dimyidae in the superfamily Pectinacea, which is otherwise made up entirely of monomyarian families. Newell's classification is as follows:

Order PTERIOIDA Newell, 1965

Suborder PTERIINA Newell, 1965

Superfamily PECTINACEA Rafinesque, 1815

Families PTERINOPECTINIDAE Newell, 1938; LEOPECTINIDAE Krasilova, 1959; AVICULOPECTINIDAE Meek and Hayden, 1864; DELTOPECTINIDAE Dickins, 1957; PSEUDOMONOTIDAE Newell, 1938; POSIDONIIDAE Frech, 1909; OXYTOMIDAE Ichikawa, 1958; ENTOLIIDAE Korobkov, 1960; PECTINIDAE Rafinesque, 1815; MONOTIDAE Fischer, 1887; BUCHIIDAE Cox, 1953; PLICATULIDAE Watson, 1930; SPONDYLIDAE Gray, 1826; TERQUEMIIDAE Cox, 1964; DIMYIDAE Fischer, 1886.

Neveeskaya *et al.* (1971) proposed a classification based on an analysis of shell structure and soft parts (gills and stomach) in extant bivalves. All are filter feeders, cemented or byssally attached. Their classification was:

Order PECTINOIDA Adams and Adams, 1857

Superfamily DIMYACEA Fischer, 1886

Family DIMYIDAE Fischer, 1886

Superfamily SPONDYLACEA Gray, 1826

Families TERQUEMIIDAE Cox, 1964; PLICATULIDAE Watson, 1930; SPONDYLIDAE Gray, 1826.

Yonge (1975) noted major resemblances between the mantle, shell and viscero-pedal mass in extant species of the Dimyidae and Plicatulidae and proposed the following classification:

Superfamily PLICATULACEA Yonge, 1975

Families DIMYIDAE Fischer, 1886; PLICATULIDAE Watson, 1930.

Waller (1978) disagreed with Yonge's interpretation of the ligament in the Dimyidae and Plicatulidae and offered a new interpretation of primary ligament, shell structure and soft tissue in extant species of the Pteriomorphia. Utilizing cladistic analysis a revised classification was proposed, which is adopted here:

Order OSTREOIDA Férussac, 1822

Suborder OSTREINA Férussac, 1822

Superfamily DIMYACEA Fischer, 1886

Superfamily PLICATULACEA Watson, 1930

Superfamily OSTREACEA Rafinesque, 1815

SYSTEMATIC PALAEOLOGY

Repositories of specimens. NMW, National Museum of Wales, Cardiff; BMNH, British Museum (Natural History), London; BGS, British Geological Survey, Keyworth; BCM, Bristol City Museum, Bristol; GM, Geiseltal Museum, Halle, Germany.

Superfamily DIMYACEA Fischer, 1886

Family DIMYIDAE Fischer, 1886

Genus ATRETA Etallon, 1862

Synonyms. *Diploschiza* Conrad, 1866; *Cyclostreon* Eichwald, 1868; *Dimyopsis* Bittner, 1895; (*vide* Cox 1964).

Type species. *Ostrea blandina* d'Orbigny, 1849, p. 375, from the Oxfordian of France; subsequent designation of Cox 1964, p. 45.

Range. Early Rhaetian to Campanian of Europe and North America.

Diagnosis. Small, suborbicular, often slightly oblique; right valve attached by the greater part of its surface, internally shallowly concave, bordered by a raised ridge, inner shell layer generally missing exposing inner surface of outer shell layer with divaricating or anastomosing riblets ending in some species as transverse crenulations of the raised ridge; left valve almost flat with commarginal lamellose ornament, internal of valve showing suboval dimyarian musculature, resilium pit small, crura short and thin.

Atreta intusstriata (Emmrich, 1853)

Plate 1, figs 1-10

- + .1851 *cf. Ostrea placunoides* Munster; Schafhäütl, p. 413, pl. 7, fig. 7a-c.
- v*1853 *Ostrea intusstriata* Emmrich, p. 377.
- .1855 *Spondylus liasimus* Terquem, p. 327, pl. 23, fig. 7a-d.
- .1861 *Ostrea interstriata* Emmrich; Moore, p. 501, pl. 16, fig. 25.

- .1864 *Plicatula intus-striata* (Emmrich); Dumortier, p. 74, pl. 1, figs 13–16.
 .1865 *Plicatula liasina* (Terquem); Terquem and Piette, p. 107, pl. 13, figs 11–13.
 .1865 *Plicatula lotharingiae* Terquem and Piette, p. 109, pl. 13, figs 14 and 15.
 .1865 *Plicatula parkinsoni* Bronn; Terquem and Piette, p. 108, pl. 13, fig. 16.
 .1866 *Plicatula intusstriata* (Emmrich); Capellini, p. 484, pl. 6, fig. 12.
 .1867 *Plicatula intusstriata* (Emmrich); Stefano, p. 147, pl. 6, figs 35 and 36.
 .1876 *Plicatula liasina* (Terquem); Tate and Blake, p. 369.
 1884 *Spondylus liassimus* (Terquem); Simpson, p. 178.
 1884 *Spondylus intus-striatus* Tate; Simpson, p. 178.
 1893 *Plicatula intusstriata* (Emmrich); Greco, p. 128.
 1907 *Plicatula intusstriata* (Emmrich); Joly, p. 23.
 1916 *Dimyopsis (Plicatula) intusstriata* (Emmrich); Goetel, p. 158.
 1917 *Plicatula (Atreta) intusstriata* (Emmrich); Rollier, p. 536.
 1917 *Plicatula (Atreta) lotharingiae* (Terquem and Piette); Rollier, p. 536.
 1917 *Plicatula (Atreta) liasina* (Terquem); Rollier, p. 536.
 1917 *Plicatula (Atreta) ambigua* Rollier, p. 537.
 1929 *Plicatula (Dimyopsis) intusstriata* (Emmrich); Lanquine, p. 60.
 .1933 *Dimyodon intus-striatus* (Emmrich); Arkell, pl. 29, fig. 5.
 1936 *Plicatula intusstriata* (Emmrich); Joly, p. 95.

Lectotype. Designated herein; GM MLU2/GM/HS.1, (plaster cast NMW 90.16G.2) attached right valve from the ‘Gervillienbildung’ (Rhaetian) of Kössen, Austria.

Dimensions. Height 11 mm, length 9 mm, anterior length 4 mm.

Paralectotypes. GM MLU1/GM/HS.1–10, (plaster cast NMW 90.16G.1) from the ‘Gervillenschichten’ (Rhaetian) of Sonntagshorn mountain, Bavaria, Germany; GM MLU3/GM/HS, (plaster cast NMW 90.16G.3) from the ‘Gervillienbildung’ (Rhaetian) of Eipelgraben bei Staudach, Bavaria, Germany; GM MLU2/GM/HS.2, details as lectotype.

Material. NMW 15.131.G9; NMW 20.349.G10; NMW 20.349.G16; NMW 20.362.G47; NMW 22.345.G384; NMW 22.345.G387–390; NMW 22.345.G392; NMW 22.345.G401–409; NMW 46.311.G12; NMW 65.345.GR26; NMW 67.121.G88; NMW 67.121.G138; NMW 83.22G.145–152; NMW 83.22G.174; NMW 83.22G.176–182; NMW 90.16G.1–3; BMNH L77133; BMNH L77176; BMNH L77194–L77195; BMNH L18104; BGS Zd14; BGS 312; BGS 91845–91863; BCM 9964 (9 specimens).

Stratigraphical range. Early Rhaetian – early Sinemurian (*resupinatum* Subzone)

Geographical range. United Kingdom (Moore 1861; Tate and Blake 1876; Simpson 1884; Arkell 1933; Hodges 1987), France (Terquem 1855; Dumortier 1864; Terquem and Piette 1865), Belgium (Joly 1907, 1936), Germany (Goetel 1916), Austria (Schafhäütl 1851), Italy (Capellini 1866; Stefano 1867; Greco 1893)

Description. Externally oyster-like, generally small, suborbicular to subovate in outline, often oblique, inequivalve, inequilateral, hinge line straight to slightly convex; right valve attached by most of its surface area, hinge area rarely preserved; left valve rather flattened often following the contours of the underlying attached valve, with external ornament of commarginal imbrications, valve margins closed.

Internally, right valve shallowly concave with raised ridge around the shell margin; inner shell layer missing exposing inner surface of outer shell layer with ornament of numerous divaricating anastomosing fine riblets, number increases with size, with up to four orders of bifurcation, originating at the umbo and terminating at the margin of the raised ridge, giving a crenulated appearance on the crest of the raised ridge. No hinge structures or muscle scars seen. Left valve has dimyarian musculature, anterior adductor muscle scar suboval in outline, posterior adductor slightly larger, suborbicular in outline and bilobed, muscle scars symmetrically positioned at about one third of the height below hinge line. Hinge structures not seen.

Remarks. Emmrich’s (1853, p. 376) description made no direct reference to any type material. He mentioned only that his species was widespread in the ‘Gervillienbildung’ (Rhaetian) of the Austrian Alps and was found at Partenkirchen, Kreuth and Sonntagshorn mountain. His main

collection housed at the Geiseltal Museum, Martin-Luther Universität, Wittenberg, Halle, Germany, contains three limestone blocks collected from Sonntagshorn, Kössen and a locality near Staudach (pers. comm. Dr G. Krumbiegel). One block (GM MLU1/GM/HS) has one syntype, a second (GM MLU2/GM/HS) two syntypes, and the last (GM MLU3/GM/HS) has ten specimens encrusted on '*Ostrea haidingeriana*' Emmrich.

Schafhäütl (1851) described and figured three right valves of this species from the Rhaetian of the southern Bavarian Alps, and compared them with the Muschelkalk species *Ostrea placunoides* Munster; he did not erect a name. His specimens were housed in the Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich but were destroyed during the Second World War. Emmrich (1853) made reference to Schafhäütl's description when describing material he collected from the Rhaetian of the Austrian Alps which he named *Ostrea intusstriata*. Although he produced no figure of his species, his description mentions quite clearly the anastomosing riblets on the inside of the attached right valve and their termination on the raised ridge at the shell margin. There can be little doubt, from the features he described and from his reference to Schafhäütl's description and figures, that his material is conspecific with specimens common in the Rhaetian and Lower Lias of Europe.

In Terquem's (1855) description of *Spondylus liasinus* mention is made of two cardinal teeth and muscle impressions below the beaks. A further mention of two cardinal teeth was made by Terquem and Piette (1865) when describing their *Plicatula lotharingiae*.

The shape of the muscle scars in this species and in particular the bilobed posterior adductor show a close resemblance to those seen in the extant species *Basiliomya goreauii* Bayer, 1971 and *Dimya corrugata* Hedley, 1902. Both these species belong to the Dimyidae; they were discussed in full by Yonge (1978). This provides further evidence of the close relationship between *Atreta intusstriata* and extant species of the Dimyidae.

Mode of life. It is presumed that *Atreta* was an epifaunal filter-feeder which lived permanently attached to the shells of other molluscs. It is found both in the marginal and off-shore facies of the Lower Jurassic. It has been observed encrusting the bivalves *Gryphaea arcuata*, *Pinna* (*Pinna*) *similis*, *Plagiostoma giganteum* and *Antiquilima succincta*. Large shells such as *Plagiostoma* can exhibit encrusted *Atreta* to a density of up to twenty per 0.01 sq. m. It is often found in association with other encrusting bivalves such as species of *Liostrrea*.

EXPLANATION OF PLATE I

Figs 1–10. *Atreta intusstriata* (Emmrich). 1, lectotype GM MLU2/GM/HS. 1, (plaster cast NMW 90.16G.2), internal of right valve; 'Gervillienbildung' (Rhaetian); Kössen, Austria. 2, paralectotype GM MLU2/GM/HS.2; details as in 1. 3, NMW 83.22G.182; internal of right valve attached to *Plagiostoma giganteum* Sowerby, showing anastomosing riblets; *bucklandi* Zone, Lower Lias; between Cwm Nash and Nash Point, South Glamorgan, South Wales. 4, paralectotype GM MLU1/GM/HS, (plaster cast NMW 90.16G.1); internal of right valve; 'Gervillienbildung' (Rhaetian); Sonntagshorn Mountain, Bavaria, Germany. 5, NMW 83.22G.182; external view of left valve attached in life position, details as in 3. 6, NMW 83.22G.178; internal of right valve attached to *Plagiostoma giganteum* Sowerby; *bucklandi* Zone, Lower Lias; 1.6 km E of Nash Point, South Glamorgan, South Wales. 7, paralectotypes GM MLU3/GM/HS.1–3, (plaster cast NMW 90.16G.3); internal of right valves attached to '*Ostrea haidingeriana*' Emmrich; 'Gervillienbildung' (Rhaetian); Eipelgraben bei Staudach, Bavaria, Germany. 8, paralectotypes GM MLU3/GM/HS.4–5; detail as in 7. 9, paralectotype GM MLU3/GM/HS.5; detail as in 7. 10a, NMW 83.22G.174; silicified left valve internal showing dimyarian musculature; *semicostatum* Zone, Lower Lias; temporary excavation 400 m N of Ford Motor Company site, Bridgend, Mid Glamorgan, South Wales. 10b, Detail as in 10a; dimyarian muscle scars highlighted for clarity, showing anterior adductor and bilobate posterior adductor. Magnifications: 1–8, $\times 2$; 9, $\times 3$; 10a, b, $\times 4$.

All specimens were coated with ammonium chloride prior to photographing, with the exception of figure 10.



1



2



3



4



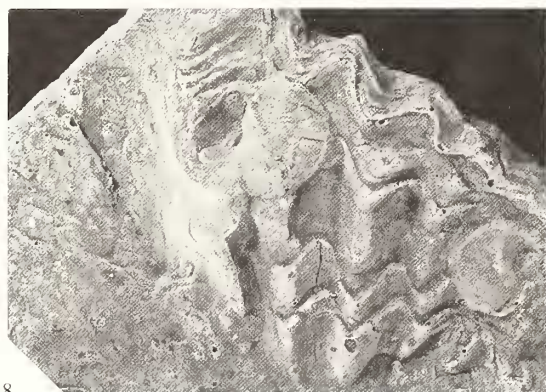
5



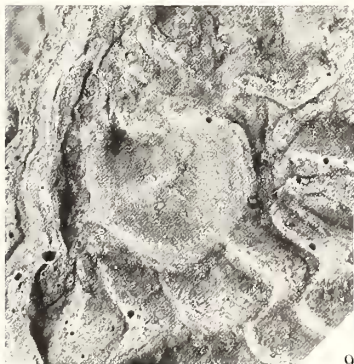
6



7



8



9



10 a



10 b

DISCUSSION

The evidence presented here of dimyarian musculature in *Atreta* confirms the observations of Etallon (1862). The assignment of this genus to the monomyarian Plicatulidae by Cox (1964) is therefore incorrect. *Atreta* is transferred to the Dimyidae based on the diagnostic characteristics described and also on the close similarity with musculature in modern species of this family. The stratigraphical range of the Dimyidae is thus extended back to the early Rhaetian.

Although an entire specimen with conjoined valves has been observed (NMW.83.22G.182), the left valve of members of this genus is rarely seen. Therefore they are known almost exclusively by the attached right valves, which due to preservation generally lack any evidence either of musculature or dentition, almost certainly a result of the loss of an aragonitic shell layer. This opinion has been given previously by Eudes-Deslongchamps (1860) and Cox (1964). Stenzel (1964) showed that the prodissoconch of the oyster *Crassostrea virginica* (Gmelin) is aragonitic, whereas the adults are mainly calcitic. This adds further credence to the possibility of shell layer loss in *Atreta*.

Atreta intusstriata (Emmrich) reached its highest population density in the Rhaetian of Europe where it was often used as a stratigraphical indicator. On the evidence of this species alone Lower Lias beds have been incorrectly designated as Rhaetian.

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